
XXXV. *On the Organs and Mode of Fecundation in Orchideæ and Asclepiadeæ. By Robert Brown, Esq., V.P.L.S., &c.*

Read November 1 *and* 15, 1831.

In the Essay now submitted to the Society, my principal object is to give an account of some observations, made chiefly in the course of the present year, on the structure and economy of the sexual organs in Orchideæ and Asclepiadeæ,—the two families of phænogamous plants which have hitherto presented the most important objections to the prevailing theories of vegetable fecundation.

But before entering on this account, it is necessary to notice the various opinions that have been held respecting the mode of impregnation in both families: and in concluding the subject of Orchideæ, I shall advert to a few other points of structure in that natural order.

ORCHIDEÆ.

The authors whose opinions or conjectures on the mode of impregnation in Orchideæ I have to notice, may be divided into such as have considered the direct application of the pollen to the stigma as necessary: and those who,—from certain peculiarities in the structure and relative position of the sexual organs in this family,—have regarded the direct contact of these parts as in many cases difficult or altogether improbable,

bable, and have consequently had recourse to other explanations of the function.

In 1760, Haller, the earliest writer of the first class, in describing his Epipactis, states that the antheræ or pollen masses, after leaving the cells in which they are originally inclosed, are retained by the process called by him sustentaculum, the rostellum of Richard, from which they readily fall upon the stigma[*]. He adds, that both in this genus and in Orchis the stigma communicates by a fovea or channel with the ovarium.

But as in 1742 he correctly describes the stigma of Orchis[†], and in his account of Epipactis[‡] notices also the gland derived, as he says, from the sustentaculum, and which is introduced between and connects the pollen masses, his opinion on the subject, though not expressed, is distinctly implied even at that period: or as indeed it may be said to have been so early as 1736[§], when he first described the channel communicating with the ovarium, and considered it as being in the place of a style.

In 1763, Adanson[||] states that the pollen masses are projected on the stigma, of which his description is at least as satisfactory as that of some very recent writers on the subject. He also describes the flower of an Orchideous plant as being monandrous, with a bilocular anthera, containing pollen which coheres in masses (a view of structure first entertained, but not published, by Bernard de Jussieu[¶]); and he correctly marks the relation both of the stamen and placentæ of the ovarium to the divisions of the perianthium.

In 1777, Curtis, in the Flora Londinensis in his figure and account of *Ophrys apifera*, correctly delineates and describes the pollen masses, called by him antheræ, the glands at their base inclosed in distinct cuculli or bursiculæ, and the stigma, with the surface of which he represents the masses as coming in contact.

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[*] *Orchid. class. constitut. in Act. Helvet.* iv. p. 100.

[†] *Hall. Enum.* p. 262.

[‡] *Id.* p. 274.

[§] *Meth. stud. bot.* p. 21.

[||] *Fam. des Plant.* ii. p. 69.

[¶] *Juss. gen. pl.* p. 66.

In his second volume, the two lateral adnate lobes of the stigma, and the auriculæ of the column of *Orchis mascula*, are distinctly shown; and these auriculæ, now generally denominated rudimentary stamina, are also delineated in some other species of Orchis afterwards figured in the same work.

In 1793, Christian Konrad Sprengel[*] asserts that the pollen masses are applied directly to the secreting or viscid surface on the front of the column, in other words to the stigma, and that insects are generally the agents in this operation.

In 1799, J. K. Wachter[†] supports the same opinion, as far as regards the necessity of direct contact of the pollen masses with the female organ; and this observer was the first who succeeded in artificially impregnating an Orchideous plant, by applying the pollen to the stigma of *Habenaria bifolia*.

In 1799 also, or beginning of 1800, Schkuhr[‡] takes the same view of the subject, and states that the pollen masses, which resist the action of common moisture, are readily dissolved by the viscid fluid of the stigma.

In 1800 Swartz[§], in adopting the same opinion, notices various ways in which the application of the pollen may be effected in the different tribes of this family, repeats the statement of Schkuhr on the solvent power of the stigma, and in *Bletia Tankervilliæ* describes ducts which convey the absorbed fluid from that organ to the ovarium.

In 1804, Salisbury[||] asserts that he had succeeded in impregnating many species belonging to different tribes of Orchideæ, by applying the pollen masses to the stigma, whose channel communicating with the cavity of the ovarium, and first noticed by Haller, he also describes.

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[*] *Entd. Geheim.* p. 401.

[†] *Römer Archiv.* ii. p. 209.

[‡] *Handbuch* iii. p. 192.

[§] *Act. Holm.* 1800 p. 134.

[||] *Linn. Soc. Transact.* vii. p. 29.

In 1827, Professor L. C. Treviranus* published an account of several experiments made by him in 1824, which satisfactorily prove that impregnation in this family may be effected by the direct application of the pollen to the stigma.

About the end of 1830 a letter from Professor Amici† to M. Mirbel was published, in which that distinguished microscopical observer asserts that in many phænogamous plants the pollen tubes, or *boyaux*, penetrate through the style into the cavity of the ovarium, and are applied directly to the ovula.

In this important communication Orchideæ are not mentioned, but M. Adolphe Brongniart in a note states that he himself has seen the production of *boyaux* or pollen tubes even in this family; that here, however, as well as in all the other tribes in which he had examined these tubes, he found them to terminate in the tissue of the stigma.

Of the second class of authors the earliest is Linnæus‡, who, in 1764, not satisfied either with his own or any other description then given of the stigma, inquires whether the influence of the pollen may not be communicated internally to the ovarium.

In 1770, Schmidel§, in an account which he gives of a species of Epipactis, describes and figures the upper lip of the stigma, the rostellum of Richard, with its gland both before and after the bursting of the anthera; and as he denominates that part, before the pollen masses are attached to it, "stigma virgineum," he may be considered as belonging to the same class.

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* *Zeitschrift f. Physiol.* ii. p. 225.

† *Annal. des Sc. Nat.* xxi. p. 329.

‡ *Prælect. in Ord. Nat. ed. Giseke.* p. 182.

§ *Gesn. Op. Bot. hist. plant.* fasc. ii. p. 15. tab. 19.

Koelreuter, the next writer in point of time, and whose essay was published before Linnæus's query appeared, states, in 1775*, that the pollen masses, which he denominates naked antheræ, impart their fecundating matter to the surface of the cells of the true anthera, regarded by him consequently as stigma, and that through this surface it is absorbed and conveyed to the ovarium.

In 1787, Dr. Jonathan Stokes† conjectures that in Orchideæ, as well as in Asclepiadeæ, the male influence, or principle of arrangement, as it is termed by John Hunter, may be conveyed to the embryo without the intervention of air: a repetition certainly of Linnæus's conjecture, with which however, as it was not published till 1791, he could not have been acquainted.

In 1791, Batsch‡ states that in Orchis and Ophrys,—and his observation may be extended at least to all Satyrinæ or Ophrydeæ,—the only way in which the mass of pollen can act on the ovarium, is by the retrogradation of the impregnating power through the pedunculus or caudicula of the pollen mass to the gland beneath it, which he is disposed to refer rather to the stigma than to the anthera.

The late Professor Richard, in 1802§, expressly says that fecundation is operated in Orchideæ and Asclepiadeæ without a change of place in the stamina; his opinion therefore must be considered identical with that of Batsch, and extended to the whole order.

It might perhaps be inferred from the description which I gave of Orchideæ in a work published in 1810‖, that my opi-

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* *Act. Phys. Palat.* iii. p. 55.

† *With. Bot. Arrang.* 2nd ed. ii. p. 964.

‡ *Botanische Bemerk.* i. p. 3.

§ *Dict. de Botan. par Bulliard* ed. 2. p. 56.

‖ *Prodr. Flor. Nov. Holl.* i. p. 310.

nion respecting the mode of impregnation agreed with that of Batsch and Richard, though it is not there actually expressed, nor indeed very clearly in another publication of nearly the same date*, in which I had adverted to this family. But I have since on several occasions more explicitly stated that opinion, which, until lately, I always considered the most probable hypothesis on the subject. At the same time its probability in this family appeared to me somewhat less than in Asclepiadeæ. For in Orchideæ a secreting surface in the female organ, apparently destined to act on the pollen without the intervention of any other part, is manifest; and some direct evidence of the fact existed, though not then considered satisfactory. In Asclepiadeæ, however, I entertained hardly any doubt on the subject; the only apparently secreting surface of the stigma in that family being occupied by the supposed conductors of the male influence, and no evidence whatever, with which I was acquainted, existing of its action through any other channel.

In 1816 or 1818 I received from the late celebrated Aubert du Petit Thouars some printed sheets of an intended work on Orchideæ, which, with a few alterations, was completed and published in 1822†.

From the unfinished work, as well as that which was afterwards published, it appears that this ingenious botanist considered the glutinous substance connecting the grains or lobules of pollen as the "aura seminalis" or fecundating matter; that the elastic pedicel of the pollen mass, existing in part of the family, but according to him not formed before expansion, consists of this gluten; and that in the expanded flower the gluten which has escaped from the pollen is, in all cases, in communication with the stigma.

He describes the stigma as forming on the surface of the column a glutinous disk, from which a central thread or cord of the same nature is continued through the style to the cavity of the ovarium, where it divides into three branches, and that each of these is again subdivided into two. The six branches thus formed, are closely applied to the parietes of the ovarium, run down one on each side of the corresponding placenta to its base, each giving off numerous ramuli, which spread themselves among the ovula, and separate them into irregular groups.

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* *Linn. Soc. Transact.* x. p. 19.

† *Hist. des Orchid.* p. 14.

Hence, according to this author, a communication is established between the anthera and the ovula, which he adds are impregnated through their surface, and not, as he supposes to be the case in other families, through their funiculus or point of attachment to the placenta.

The remarkable account of the stigma here quoted, though coming from so distinguished and original an observer, and one who had particularly studied this family of plants, seems either to have been entirely overlooked, or in some degree discredited by more recent writers, none of whom, as far as I can find, have even alluded to it. And I confess it entirely escaped me until after I had made the observations which will be stated in the present essay, and which confirm its accuracy as to the existence and course of the parietal cords, though not as to their nature and origin.

In 1824 Professor Link[*] expresses his opinion that the rostellum of Richard is without doubt the true stigma.

In 1829 Mr. Lindley[†], who for several years has particularly studied and has lately published part of a valuable systematic work on Orchideous Plants, states that in this family impregnation takes effect by absorption from the pollen masses through their gland into the stigmatic channel.

In 1830, in his Introduction to the Natural System of Botany, the same statement is repeated; and in this work it also appears that he regards the glands to which the pollen masses become attached in Ophrydeæ as derived from the stamen, and not belonging to the stigma*, as in 1810 I had described them. It would even appear, from a passage in his systematic work† published in the same year, that he considers the analogous glands, existing in most other tribes of Orchideæ, as equally belonging to the stamen: in his "Introduction," however, he refers them to the stigma in all cases except in Ophrydeæ.

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[*] *Philos. Bot.* p. 298.

[†] *Synops. Brit. Flor.* p. 256.

Towards the end of 1830 the first part of Mr. Francis Bauer's Illustrations of Orchideous Plants, edited by Mr. Lindley, was published.

From this work, of the importance and beauty of which it is impossible to speak too highly, it may be collected that Mr. Bauer's opinion or theory of impregnation in Orchideæ does not materially differ from that of Batsch, Richard, and other more recent writers. From one of the figures it appears that this theory had occurred to him as early as 1792; and in another figure, bearing the same date, he has accurately represented the structure of the grains of pollen in a plant belonging to Ophrydeæ, a structure which I had not ascertained in that tribe till 1806. Although Mr. Bauer's theory is essentially the same as that of Batsch and Richard, yet there are some points in which it may be considered peculiar; and chiefly in his supposing impregnation to take effect long before the expansion of the flower, at a time when the sexual organs are so placed with relation to each other that the fecundating matter, believed by him to pass from the pollen mass through its caudicula, where that part exists, to the gland attached to it, may be readily communicated to the stigma, with which the gland is then either in absolute contact or closely approximated. The more important points of this account may be extended to nearly the whole order, but it is strictly applicable only to Satyrinæ or Ophrydeæ, a tribe in which Mr. Bauer seems, with Mr. Lindley, to consider the glands as belonging to the stamen and not to the stigma*. In those genera of this tribe in which the glands are included in a pouch or bursicula, he describes and figures perforations in the back of the pouch, through which the fecundating matter is communicated from the glands to the stigma; and one of the figures is intended to represent a gland in the act of parting with the fecundating matter.

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* "The pollen is not less curious. Now we have it in separate grains, as in other plants, but cohering to a mesh-work of cellular tissue, which is collected into a sort of central elastic strap; now the granules cohere in small angular indefinite masses, and the central elastic strap becomes more apparent, has a glandular extremity, which is often reclined in a peculiar pouch especially destined for its protection."—*Introduct. to Nat. Syst. of Bot.* p. 263.

† *Gen. and Sp. of Orchid.*, Part I. p. 3.

It is impossible to judge correctly of Mr. Bauer's theory until all the proofs and arguments in its favour are adduced. I may observe, however, that those already published are by no means satisfactory to me.

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* In the second part of Mr. Bauer's Illustrations, which has appeared since this paper was read, the explanation of Tab. 3. fig. 6. is corrected in the following manner:

" *For* 6. A pollen mass with its caudicula and gland taken out of the anther;

" *Read* 6. A pollen mass with its caudicula and the internal socket of the stigmatic gland."

It is evident, indeed, in the second part of the Illustrations, from figures 8, 9, 11, and 12, of Tab. 12. representing details of *Satyrium pustulatum,* and the drawings of which were made in 1800, that Mr. Bauer must, from that time at least, have correctly understood the origin of the glands in Ophrydeæ. There is nothing, however, in any of the figures in Tab. 3. of the first part at variance with their explanations, from which I judged of his opinion. It may therefore be concluded that Mr. Bauer had not examined these explanations before their publication.

For, in the first place, in the very early stage in which, according to this theory, impregnation is supposed to be effected, it appears to me that the pollen is not in a state to impart its fecundating matter, nor the stigma to receive it; and it may be added, though this is of less weight, that the ovula have neither acquired the usual degree of development, nor that position which they afterwards take, and which gives the apex of the nucleus or point of impregnation the proper direction, with regard to the supposed impregnating surface.

Secondly, in the figure which may be said to exhibit a demonstration of the correctness of the theory,—in that, namely, representing the gland in the act of parting with the fecundating matter,—the magnifying power employed (which is only fifteen times,) is surely insufficient for the establishment of a fact of this kind; while the disengagement of minute granules, which no doubt often takes place when the gland is immersed in water, may readily be accounted for in another way*.

Thirdly, I have never been able to find those perforations, represented by Mr. Bauer, in the bursiculæ of Orchis and Ophrys, and the existence of which in these genera is essential to his hypothesis.

And, lastly, the appearance of the stigma in *Bletia Tanker-*

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* This second observation ought not now to be taken into account, as in the second part of Mr. Bauer's Illustrations the following correction occurs respecting the figure alluded to (Tab. 3. fig. 8.)

"This is in some measure an ideal figure to represent in what way the fecundating matter is supposed to leave the caudicula and stigmatic gland; for this reason there has been no attention paid to preserving a proportion between the pollen mass and the fecundating matter."

I may here, however, remark, that it was evidently not my intention, in the observation in question, to throw any doubt on the correctness of Mr. Bauer's figure, being aware that very minute granular matter, separating from the gland when immersed in water, is actually visible with a lens of about half an inch focus. I objected to it only as a satisfactory proof of the theory referred to.

villiæ, after impregnation, as he believes, according to my view of the subject would rather prove that it was in a state capable of acting upon, but had not yet received the fecundating matter from, the anthera.

In thus venturing to differ from so accurate and experienced an observer as Mr. Bauer on a subject which he has for many years minutely studied and so beautifully illustrated, I am well aware how great a risk I incur of being myself found in error.

I am very desirous, however, that the perusal of this sketch of the various statements that have appeared on the question of impregnation, with the greater part of which he is at present probably unacquainted, should induce him to reexamine the facts and arguments by which his own opinion on this subject is supported. He will thus either succeed in establishing his theory on more satisfactory grounds, or, if the examination should prove unfavourable, he will, I am persuaded, from his well known candour, as readily abandon it.

The notice here given of the opinions of botanists on impregnation in Orchideæ brings the subject down to the spring of the present year, when from circumstances, which I may hereafter have occasion to advert to, my attention was directed to this family of plants, the particular study of which I had for a long time discontinued.

In reviewing notes respecting them, made many years ago, I found some points merely hinted at, or imperfectly made out, which seemed deserving of further examination; and in the course of these inquiries, other observations of at least equal importance suggested themselves.

I now proceed to state, in some cases briefly, in others at greater length, the results of this investigation.

The first question that occupied me was, the relation which the lateral and generally rudimentary stamina bear to the other parts of the flower.

Into this subject I had in part entered in my Observations on Apostasia, published by Dr. Wallich in his "Plantæ Asiaticæ Rariores*," and had then considered it probable that in all cases these Stamina, in whatever state of development they were found, belonged to a different series from the middle and usually fertile stamen; in other words, were placed opposite to the two lateral divisions of the inner series of the perianthium. In 1810, however, when I first advanced my hypothesis of the true nature of these processes of the column, I supposed, though the opinion was not then expressed, that they formed the complement of the outer series of stamina; a view which has been since very generally adopted, especially by Dr. Von Martius, who has given it in a stenographic formula, and by Mr. Lindley, who has exhibited the relative position of parts in this family in a diagram†. A careful examination of the structure of the column in various tribes of the order, chiefly by means of transverse sections, has fully confirmed the opinion I entertained when treating of Apostasia; and more particularly established the fact in Cypripedium, in which these lateral stamina are perfectly developed.

On the hypothesis of rudimentary stamina I may remark, that it presented itself to me some time before the publication of the Prodromus Floræ Novæ Hollandiæ; and my belief is, that until the appearance of that work this view had not been taken by any other observer in England. Mr. Bauer at least, in a recent conversation on the subject, readily admitted, with his usual candour, that although acquainted with a case of accidental development, the general view had not occurred to him until stated by me.

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* Vol. i. p. 74.

† *Introduct. to Nat. Syst.* p. 264.

In my mind it arose from contrasting the structure of Cypripedium with those genera of New Holland Orchideæ—Diuris, Prasophyllum, and others—in which the lateral processes or appendages of the column are so remarkably developed; and I afterwards, in searching for additional confirmations of the hypothesis, believed I had found such in the more minute lateral auriculæ of the column present in most Ophrydeæ.

These auriculæ however, though they might serve to confirm, would hardly have suggested the hypothesis, at the period especially of which I speak. They had indeed until then been altogether overlooked, except by Malpighi*, by Curtis in his Flora Londinensis, perhaps in Walcott's Flora Britannica, and by Mr. Bauer, whom they were not likely to escape.

In my recent observations on Apostasia, referred to, I noticed a singular monstrosity of *Habenaria bifolia*, which, if such deviations from ordinary structure are always to be trusted, would throw great doubt on the hypothesis being applicable to these auriculæ of Ophrydeæ. For in this case, in which three antheræ are formed, auriculæ not only exist on the middle or ordinary stamen, but one is also found on the upper side of each of the lateral antheræ, which are here opposite to two divisions of the outer series of the perianthium. I have lately met with another instance of a similar monstrosity equally unfavourable; and I may add that this doubt is still further strengthened by my not being able to find vascular cords connected with these auriculæ in the only plants of Ophrydeæ in which I have carefully examined, with this object, the structure of the column, namely, *Orchis Morio*, *mascula*, and *latifolia*.

I do not indeed regard the absence of vessels as a complete proof of these auriculæ not being rudimentary stamina. But I may remark, that in the other tribes of Orchideæ, in many of whose genera analogous processes are found, and in which tribes alone cases of their complete development have hitherto been observed, vessels not only generally exist in these processes, but may often be traced to their expected origins, namely, into those cords which also supply the inner lateral divisions of the perianthium.

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* *Op. Om.* tab. 25. fig. 142.

Although not necessarily connected with my subject, I may here advert to the remarkable monstrosity in the flowers of an *Ophrys* described and figured by M. His* upwards of two years before the appearance of my Prodromus. This account I did not meet with till after that part of the volume relating to Orchideæ was printed; and I have here only to observe respecting it, that neither the monstrosity itself, consisting of the conversion into stamina of the three inner divisions of the perianthium, nor the author's speculation founded on it, has any connexion with my opinion which relates to the processes of the column.

M. His's paper, however, and the remarkable structure of *Epistephium* of M. Kunth, have together given rise to a third hypothesis, whose author, M. Achille Richard†, considers an Orchideous flower as generally deprived of the outer series of the perianthium, which is present only in Epistephium. He consequently regards the existing inner series of perianthium, or that to which the labellum belongs, as formed of metamorphosed stamina.

This hypothesis, although apparently sanctioned by the structure of Scitamineæ, I consider untenable; the external additional part in Epistephium, which I have examined, appearing to me rather analogous to the calyculus in some Santalaceæ, in a few Proteaceæ, and perhaps to that of Loranthaceæ.

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* *Journal de Physique,* lxv. (1807), p. 241.

† *Mém. de la Soc. d'Hist. Nat. de Paris,* iv. p. 16.

With reference to the support the hypothesis may derive from the monstrosity described by M. His, I may add that I have met with more than one case of similar conversion into stamina of the inner series of the perianthium, or at least of its two lateral divisions, with a manifest tendency to the same change in the labellum: and in one of these cases, namely *Neottia picta*, in addition to the conversion of the two lateral divisions of the perianthium, the lateral processes of the column were also completely developed.

The next point examined was the composition of the Stigma with the relation of its lobes or divisions to the other parts of the flower, and especially to the supposed component parts of the ovarium. On this subject very little information is to be obtained from the writings of botanists, most of whom have contented themselves with describing the stigma as a disk, a fovea glutinosa, a secreting surface, or viscid space in front of the column. The late celebrated Richard however, who adverts to the occasional existence of two lateral processes of his gynizus, may be supposed to have had more correct notions of its composition: and it may also be observed, that in Curtis's plate of *Ophrys apifera* already referred to, and still more distinctly in Mr. Bauer's figure of *Orchis mascula*, the two lateral lobes are represented as distinct, corresponding very exactly with Haller's description, in 1742, of the stigma in this genus.

The result of my examination of this point satisfied me that Orchideæ have in reality three stigmata, generally more or less confluent, but in some cases manifestly distinct, and two of which are in several instances even furnished with styles of considerable length.

These stigmata are placed opposite to the three outer divisions of the perianthium, and consequently terminate the axes of the supposed component parts of the ovarium, always regarded by me as made up of three simple ovaria united by their ovuliferous margins; a structure in which the ordinary relation of stigmata to placentæ is that here found.

In Mr. Bauer's "Illustrations" already referred to, a very different account is given of the composition of the ovarium, which is there said to be formed of six pieces.

This view of its composition seems to be founded on the existence of six vascular cords, on the apparent interruptions in the cellular tissue, and on the singular dehiscence of the capsule. But the mere number of vascular cords, which, being destined to supply all parts of the flower, may be said rather to indicate the divisions of the perianthium than those of the ovarium, cannot be considered as affording an argument of much importance, and, if it were, would equally apply to many other families having trilocular ovaria, as Irideæ; while the interruptions or inequalities of cellular tissue may be viewed as only the preparation for that dehiscence which, though very remarkable in this order, is in a great degree analogous to that taking place in most Cruciferæ, in several Leguminosæ, and in other families of plants. It may also be objected to Mr. Bauer's view of the composition of ovarium, that the arrangement of the parietal placentæ, which on this hypothesis would occupy the axes of the three alternate component parts, is contrary to every analogy; while the position of the stigmata, if my account should prove to be correct, affords evidence nearly conclusive of the ovarium being formed of only three parts.

In those genera of Orchideæ in which the lateral stamina are perfect, and the middle stamen without anthera, namely, Cypripedium and Apostasia, all these lobes or divisions of stigma are equally developed, are of nearly similar form and texture, and, as I have proved by direct experiment in Cypripedium, are all equally capable of performing the proper function of the organ.

In most other cases the anterior lobe, or that placed opposite to the perfect stamen, and deriving its vessels from the same cord, manifestly differs both in form and texture from the other two. To this anterior, or upper lobe, as it generally becomes in the expanded flower, the glands always belong to which the pollen masses become attached, but from which they are in all cases originally distinct, as may be proved even in Ophrydeæ.

According to my view, therefore, of the mode of impregnation, its office is essentially different from that of the two lateral lobes or stigmata, which in various degrees of development are always present, and in all cases, when the ovarium is perfect, are capable of performing their proper function.

The greatest development of these lateral stigmata takes place in the tribe of Satyrinæ or Ophrydeæ, as in many species of *Habenaria*, those especially which are found near or within the tropics; and still more remarkably in *Bonatea speciosa*, a plant hardly indeed distinguishable from the same extensive genus.

It would seem that in *Bonatea* the extraordinary development and complete separation of these lateral stigmata, have effectually concealed their true nature; and accordingly they have uniformly been considered as forming parts or appendages of the labellum, with which indeed their bases cohere. That they are really stigmata, however, I have proved by a careful examination of the tissue of their secreting surface, by the action of the pollen artificially applied to this tissue, by the descent of its tubes, hereafter to be described, along the upper surface of the styles which is destitute of epidermis, and by the consequent enlargement of the ovarium. *Diplomeris* of Mr. Don*, which may also be regarded as a species of Habenaria, is another example of nearly the same kind; and the description of stigma which, in 1813, I introduced into the character of *Satyrium**, implies an analogous development in that genus.

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* *Prodr. Flor. Nepal.* p. 26.

On the relative position of stamina and stigmata in the column of an Orchideous plant, it may be remarked that there is hardly an instance of a perfectly developed stamen and stigma placed opposite to each other, and consequently deriving their vessels from the same cord.

For, in the ordinary structure of the family in which only one perfect stamen is produced, the corresponding stigma loses entirely or in great part its proper function, which it recovers, so to speak, in those cases where this stamen becomes imperfect, or is destitute of an anthera: and hence, perhaps, it may be said that to obtain in any case the complete development of the lateral stamina, and, what is of greater importance, to ensure in all cases the perfection of the lateral stigmata, these organs are never placed opposite, but uniformly alternate with each other.

The general conformation of the ovarium, with regard to the number and relative position of the parietal placentæ, and the arrangement of their numerous ovula, has long been well understood. But the early structure and evolution of the unimpregnated ovulum have not yet, as far as I know, been in any degree attended to.

In its gradual development, the ovulum exhibits a series of changes nearly agreeing with those which M. Mirbel† has described and illustrated as taking place in other families.

In the earliest state in which I have examined the ovulum in Orchideæ, it consists merely of a minute papilla projecting from the pulpy surface of the placenta. In the next stage the annular rudiment of the future testa is visible at the base of the papilliform nucleus. The subsequent changes, namely, the enlargement of the testa, the production of a funiculus, which is never vascular, and the curvature or inversion of the whole ovulum, so as to approximate the apex of its nucleus to the surface of the placenta, take place in different genera at different periods with relation to the development of the other parts of the flower. In general when the flower expands, the ovulum will be found in a state and direction proper for receiving the male influence. But in several cases, as in Cypripedium and Epipactis, genera which in many other respects are nearly allied, the ovulum has not completed its inversion, nor is the nucleus entirely covered by its testa until long after expansion, and even after the pollen has been acted on by the stigma, and its tubes have penetrated into the cavity of the ovarium.

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* *Ait. Hort. Kew.* ed. 2. vol. v. p. 196.

† *Annal. des Sc. Nat.* xvii. p. 302.;—and in *Mém. de l'Acad. des Sc. de l'Instit.* ix. p. 212.

The tissue of the perfect stigmata in Orchideæ does not materially differ from that of many other families. In the early state the utriculi composing it are densely approximated, having no fluid interposed. In the more advanced but unimpregnated state, these utriculi enlarge, and are separated from each other by a copious and generally viscid secretion. The channel of the style, or stigma, whose parietes are similarly composed, undergoes the same changes. Both these states are represented in one of Mr. Bauer's plates, who however considers the more advanced stage as subsequent to impregnation.

In the advanced but still unimpregnated state of the ovarium, the upper portions, which are in continuation with the axes of the three placentæ, but do not produce ovula, are of a texture somewhat different from that of the greater part of the cavity, but still more obviously different from that of the cavity of the style, being neither apparently secreting nor consisting of similar utriculi. A narrow line of like surface is found extending on each side of every placenta nearly as far as it is ovuliferous. The three lines occupying the upper part of the axes, and the six lines marginal to the three placentæ, may, for a reason which will hereafter appear, be called the conducting surfaces of the ovarium.

The female organ, as now described, is in a proper state to be acted upon by the pollen applied to the stigma, and for the transmission of the fecundating matter into the cavity of the ovarium, in a manner and form which I shall presently attempt to explain.

In reflecting on the whole evidence existing in favour of the direct application of the pollen mass to the stigma, and especially on the recent experiments of Professor Treviranus*, I could no longer doubt that in this manner impregnation was actually effected in Orchideæ; and the sole difficulty in my mind to its being the only way arose from adverting to a circumstance that must have been remarked by every one who has particularly attended to this family, either in Europe or in tropical regions; namely, that all the capsules of a dense spike are not unfrequently ripened: a fact which at first seems hardly reconcileable with this mode of fecundation, at least on the supposition that the pollen mass is applied to the stigma by insects.

Without going fully into the question at present, I shall here only remark, that in several such cases I have satisfied myself, by actual examination of the stigmata belonging to capsules taken at many different heights in the spike, that pollen, by whatever means, had actually been applied to them†.

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* *Zeitschrift, f. Physiol.* ii. p. 225.

† It may also be observed, that the same difficulty applies to many other cases of dense inflorescence, as to the female spikes or strobili of Coniferæ, Zamia, and Zea; in all of which the symmetry of the ripe fruit is generally perfect, although partial failures of impregnation might be at least equally expected.

Believing, therefore, this to be the only mode in which impregnation is effected, I proceeded to examine the immediate changes produced by the application of the pollen masses to the stigma.

From numerous observations and experiments made with this view, chiefly in Satyrinæ or Ophrydeæ, and Arethuseæ, not however confined to these tribes, it was ascertained that the grains of pollen, soon after being applied to the stigma, either in the entire mass or separately, produce tubes or *boyaux* analogous to those first observed in one case by Professor Amici*, and afterwards in numerous others, and in many families, by M. Adolphe Brongniart†.

In Orchideæ one tube only is emitted from the absolutely simple grain, while the number of tubes generally corresponds with that of the divisions or cells of the compound grain. These tubes are of extreme tenuity, their diameter being generally less than 1-2000th of an inch, and they acquire a great length, even while adhering to the grains producing them. From these, however, they separate generally while still involved in the secretion and mixed with the utriculi of the stigma; and I have never observed an instance of a tube with its grain attached to it lower than the tissue of the stigma. In form they are perfectly cylindrical, or of equal diameter, neither dilated at the apex nor sensibly contracted in any part of their course. I have never found them either branched or jointed; but have frequently observed apparent interruptions in the tube, probably caused by partial coagulations of the contained fluid. Even in their earliest stage, while in length hardly equal to the diameter of the grain, I have not been able to observe them to contain distinct granules in employing a magnifying power of 150. With a power of 300 or 400 indeed, extremely minute and very transparent granular matter may be detected; but such granules are very different from those which have been supposed to belong to the grains of pollen.

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* *Atti della Soc. Ital.* xix. par. 2. p. 254. *Annal. des Sc. Nat.* ii. p. 66.

† *Annal. des Sc. Nat.* xii. p. 34.

As an entire pollen mass is usually applied to the surface of the stigma, and as a great proportion of the mass so applied is acted upon by the fluid in which it is immersed, the tubes produced are generally very numerous, and together form a cord which passes through the channel of the stigma or style.

On reaching the cavity of the ovarium this cord regularly divides into three parts, the divisions being closely applied to those short upper portions of the axes of the valves which are not placentiferous; and at the point where the placenta commences each cord again divides into two branches. These six cords descend along the conducting surfaces already described when speaking of the unimpregnated ovarium, and generally extend as far as the placentæ themselves, with which they are thus placed nearly but perhaps not absolutely in contact.

The cords now described, both general and partial, seem to me to be entirely composed of pollen tubes, certainly without any mixture of the utriculi of the stigma, or, as far as I can ascertain, of the tissue of the conducting surfaces.

In two cases, namely *Ophrys apifera* and *Cypripedium spectabile*, I at one time believed I had seen tubes going off laterally from the partial cords towards the placentæ and mixing with the ovula; but I am not at present entirely satisfied with the exactness of these observations, and I have never been able to detect similar ramifications in any other case*.

That the existence of these tubes in the cavity of the ovarium is essential to fecundation in Orchideæ, can hardly be questioned. But the manner in which they operate on, or whether they come actually in contact with, the ovula, are points which still remain undetermined.

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* See Additional Observations.

I am aware that Professor Amici*, who discovered in several plants the remarkable fact of the penetration of the pollen tubes into the cavity of the ovarium, and who regards this economy as being very general, likewise believes that in all cases a pollen tube comes in contact with an ovulum. M. Du Petit Thouars also, in his account already quoted of these cords, supposed by him to belong to the stigma of Orchideæ, describes their ultimate ramifications as mixing with the ovula.

I do not however consider myself so far advanced as these observers in this very important point†; and what I shall have to adduce on the subject of Asclepiadeæ, makes me hesitate still more to adopt their statements.

I may also remark that in Orchideæ the six cords are to be met with even in the ripe capsule, in which, allowance being made for the effect of pressure, they are not materially reduced in size; and the statement by M. Du Petit Thouars, of the lateral branches separating the ovula into irregular groups, is certainly not altogether correct; these groups being equally distinct before the existence of the cords.

With regard to the question of the origin of the pollen tubes, several arguments might be adduced in favour of M. Brongniart's opinion; which is, that they belong to the inner membrane of the grain, the intimate cohesion of the two membranes being assumed in most cases, and the no less intimate union of the constituent parts of compound grains in some others. That an inner membrane does occasionally exist is manifest in the pollen of several Coniferæ, in which the outer coat regularly bursts and is deciduous; and it will hereafter appear, that the structure in Asclepiadeæ confirms the correctness of this view.

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* *Annal. des Sc. Nat.* xxi. p. 329.

† See Additional Observations.

But whatever opinion may be entertained as to the origin of the tube, it can hardly be questioned that its production or growth is a vital action excited in the grain by the application of an external stimulus. The appropriate and most powerful stimulus to this action is no doubt contact, at the proper period, with the secretion or surface of the stigma of the same species. Many facts, however, and among others the existence of hybrid plants, prove that this is not the only stimulus capable of producing the effect; and in Orchideæ I have found that the action in the pollen of one species may be excited by the stigma of another belonging to a very different tribe.

The elongation of the tubes, so remarkable in this family, and their separation from the grain long before their growth is completed, render it probable that they derive nourishment either from the particles contained in the grain, or from the conducting surfaces with which they are in contact.

The first visible effect of the action of the pollen on the stigma is the enlargement of the ovarium, which, in cases where it was reversed by torsion in the flowering state, generally untwists and resumes its original position.

Of the changes produced in the ovulum consequent to impregnation, the first consists in its enlargement merely; and in the few cases where the nucleus is at this period still partially exposed, it becomes completely covered by the testa, the original apex, but now the lower extremity of which continues open. The next change consists in the disappearance of the nucleus, probably from its acquiring greater transparency, and becoming confluent with the substance of the testa. Soon after, or perhaps simultaneously with, the disappearance of the original nucleus, and while the enlargement of the whole ovulum is gradually proceeding, a minute opake round speck, generally seated about the middle of the testa, becomes visible. The opake speck is the commencement of the future embryo. At this period, or until the opake corpuscle or nucleus has acquired more than half the size it attains in the ripe seed, a thread may be traced from its apex very nearly to the open end of the testa, or as it may be supposed, to the apex of the original nucleus of the unimpregnated ovulum.

This thread consists of a simple series of short cells, in one of which, in a single instance only however, I observed a circulation of very minute granular matter; and in several cases I have been able to distinguish in these cells that granular areola so frequently existing in the cells of Orchideous plants, and to which I shall have occasion hereafter to advert.

The lowermost joint or cell of this thread is probably the original state of what afterwards, from enlargement and deposition of granular matter, becomes the opake speck or rudiment of the future embryo.

The only appreciable changes taking place in this opake rudiment of the embryo are its gradual increase in size, and at length its manifest cellular structure.

In the ripe state it forms an ovate or nearly spherical body, consisting, as far as I have been able to ascertain, of a uniform cellular tissue covered by a very thin membrane, the base of which does not exhibit any indication of original attachment at that point; while at the apex the remains of the lower shrivelled joints of the cellular thread are still frequently visible.

This cellular body may be supposed to constitute the Embryo, which would therefore be without albumen, and whose germinating point, judging from analogy, would be its apex, or that extremity where the cellular thread is found; and consequently that corresponding with the apex of the nucleus in the unimpregnated ovulum.

The description here given of the undivided embryo in Orchideous plants as forming the whole body of the nucleus, and consequently being destitute of albumen, agrees with the account first I believe published by M. Du Petit Thouars*, and very soon after by the late excellent Richard†.

The only other remark I have to make on the fructification of this family, is, that the seed itself, as well as its funiculus, is entirely without vessels, and that the funiculus, which in the ripe seed is inserted into the testa close to one side of its open base, can hardly be traced beyond that point.

I shall conclude my observations on Orchideæ with a notice of some points of their general structure, which chiefly relate to the cellular tissue.

In each cell of the epidermis of a great part of this family, especially of those with membranaceous leaves, a single circular areola, generally somewhat more opake than the membrane of the cell, is observable. This areola, which is more or less distinctly granular, is slightly convex, and although it seems to be on the surface is in reality covered by the outer lamina of the cell. There is no regularity as to its place in the cell; it is not unfrequently however central or nearly so.

As only one areola belongs to each cell, and as in many cases where it exists in the common cells of the epidermis it is also visible in the cutaneous glands or stomata, and in these is always double,—one being on each side of the limb,—it is highly probable that the cutaneous gland is in all cases composed of two cells of peculiar form, the line of union being the longitudinal axis of the disk or pore.

This areola, or nucleus of the cell as perhaps it might be termed, is not confined to the epidermis, being also found not only in the pubescence of the surface, particularly when jointed, as in Cypripedium, but in many cases in the parenchyma or internal cells of the tissue, especially when these are free from deposition of granular matter.

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* *Hist. des Orchid.* p. 19.

† *Mém. du Mus. d'Hist. Nat.* iv. p. 41.

In the compressed cells of the epidermis the nucleus is in a corresponding degree flattened; but in the internal tissue it is often nearly spherical, more or less firmly adhering to one of the walls, and projecting into the cavity of the cell. In this state it may not unfrequently be found in the substance of the column, and in that of the perianthium.

The nucleus is manifest also in the tissue of the stigma, where, in accordance with the compression of the utriculi, it has an intermediate form, being neither so much flattened as in the epidermis, nor so convex as it is in the internal tissue of the column.

I may here remark, that I am acquainted with one case of apparent exception to the nucleus being solitary in each utriculus or cell, namely in *Bletia Tankervilliæ*.

In the utriculi of the stigma of this plant I have generally, though not always, found a second areola apparently on the surface, and composed of much larger granules than the ordinary nucleus, which is formed of very minute granular matter, and seems to be deep seated.

Mr. Bauer has represented the tissue of the stigma in this species of Bletia, both before and as he believes after impregnation; and in the latter state the utriculi are marked with from one to three areolæ of similar appearance.

The nucleus may even be supposed to exist in the pollen of this family. In the early stages of its formation at least a minute areola is often visible in the simple grain, and in each of the constituent parts or cells of the compound grain. But these areolæ may perhaps rather be considered as merely the points of production of the tubes.

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This nucleus of the cell is not confined to Orchideæ, but is equally manifest in many other Monocotyledonous families; and I have even found it, hitherto however in very few cases, in the epidermis of Dicotyledonous plants; though in this primary division it may perhaps be said to exist in the early stages of development of the pollen. Among Monocotyledones the orders in which it is most remarkable are Liliaceæ, Hemerocallideæ, Asphodeleæ, Irideæ, and Commelineæ.

In some plants belonging to this last-mentioned family, especially in *Tradescantia virginica* and several nearly related species, it is uncommonly distinct, not only in the epidermis and in the jointed hairs of the filaments*, but in the tissue of stigma, in

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* The jointed hair of the filament in this genus forms one of the most interesting microscopic objects with which I am acquainted, and that in three different ways:

1st. Its surface is marked with extremely fine longitudinal parallel equidistant lines or striæ, whose intervals are equal from about 1-15,000th to 1-20,000th of an inch. It might therefore in some cases be conveniently employed as a micrometer.

2ndly. The nucleus of the joint or cell is very distinct as well as regular in form, and by pressure is easily separated entire from the joint. It then appears to be exactly round, nearly lenticular, and its granular matter is either held together by a coagulated pulp not visibly granular,—or, which may be considered equally probable, by an enveloping membrane. The analogy of this nucleus to that existing in the various stages of development of the cells in which the grains of pollen are formed in the same species, is sufficiently obvious.

3rdly. In the joint when immersed in water, being at the same time freed from air, and consequently made more transparent, a circulation of very minute granular matter is visible to a lens magnifying from 300 to 400 times. This motion of the granular fluid is seldom in one uniform circle, but frequently in several apparently independent threads or currents: and these currents, though often exactly longitudinal and consequently in the direction of the striæ of the membrane, are not unfrequently observed forming various angles with these striæ. The smallest of the threads or streamlets appear to consist of a single series of particles. The course of these currents seems often in some degree affected by the nucleus, towards or from which many of them occasionally tend or appear to proceed. They can hardly however be said to be impeded by the nucleus, for they are occasionally observed passing between its surface and that of the cell; a proof in the cells of the ovulum even before impregnation, and in all the stages of formation of the grains of pollen, the evolution of which is so remarkable in those species of Tradescantia*.

The few indications of the presence of this nucleus, or areola, that I have hitherto met with in the publications of botanists, are chiefly in some figures of epidermis, in the recent works of Meyen and Purkinje, and in one case in M. Adolphe Brongniart's memoir on the structure of leaves. But so little importance seems to be attached to it, that the appearance is not always referred to in the explanations of the figures in which it is represented. Mr. Bauer however, who has also figured it in the utriculi of the stigma of *Bletia Tankervilliæ*, has more particularly noticed it, and seems to consider it as only visible after impregnation.

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proof that this body does not adhere to both sides of the cavity, and also that the number and various directions of the currents cannot be owing to partial obstructions arising from the unequal compression of the cell.

* In the very early stage of the flower bud of *Tradescantia virginica*, while the antheræ are yet colourless, their loculi are filled with minute lenticular grains, having a transparent flat limb, with a slightly convex and minutely granular semi-opake disk. This disk is the nucleus of the cell, which probably loses its membrane or limb, and, gradually enlarging, forms in the next stage a grain also lenticular, and which is marked either with only one transparent line dividing it into two equal parts, or with two lines crossing at right angles, and dividing it into four equal parts. In each of the quadrants a small nucleus is visible; and even where one transparent line only is distinguishable, two nuclei may frequently be found in each semicircular division. These nuclei may be readily extracted from the containing grain by pressure, and after separation retain their original form.

In the next stage examined, the greater number of grains consisted of the semicircular divisions already noticed, which had naturally separated, and now contained only one nucleus which had greatly increased in size.

In the succeeding state the grain apparently consisted of the nucleus of the former stage considerably enlarged, having a regular oval form, a somewhat granular surface, and originally a small nucleus. This oval grain continuing to increase in size, and in the thickness and opacity of its membrane, acquires a pale yellow colour, and is now the perfect grain of pollen.

The second point of structure in Orchideæ to which I shall at present more briefly advert, is the frequent existence, particularly in the parasitical tribes, of fibrous or spirally striated cells in the parenchyma, especially of the leaves, but also in the white covering of the radical fibres.

In the leaves, they are either short spirally striated cells whose longer diameter is at right angles to the surface, as in *Stelis* and *Pleurothallis*, and whose fibres or striæ are connected by a broader membrane; or, being greatly elongated and running in the direction of the leaf, resemble compound spiral vessels of enormous diameter, and consisting entirely of the spiral fibres with no visible connecting membrane: the real spiral vessels in the same species being, as they generally are in the family, very slender and simple. In the white covering of the radical fibres the shorter striated cell is met with in many genera, especially I think in Oncidium and Epidendrum, in one species of which they have been remarked and figured by Meyen*.

My concluding observation on Orchideæ relates to the very general existence and great abundance, in this family, of Raphides or acicular crystals in almost every part of the cellular tissue.

In each cell where they exist these crystals are arranged in a single fasciculus, which is generally of a square form.

The individual crystals,—which are parallel to each other,—are cylindrical, with no apparent angles, and have short and equally pointed extremities.

The abundance of these fasciculi of crystals in the cellular tissue of the auriculæ of the column or supposed lateral stamina in Ophrydeæ, is very remarkable, giving these processes externally a granular appearance, which has been noticed though its cause seems to have been overlooked.

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* *Phytotomie*, tab. 11. f. 1 & 2.

In the recent work of Meyen*, also, some examples of these crystals in Orchideæ are given.

ASCLEPIADEÆ.

The various statements and conjectures on the structure and functions of the sexual organs in this family were collected, and published in 1811, by the late Baron Jacquin, in a separate volume, entitled, "Genitalia Asclepiadearum Controversa."

To this work, up to the period when it appeared, I may refer for a complete history, and to the tenth volume of the Linnean Society's Transactions, along with the first of the Wernerian Natural History Society's Memoirs, published somewhat earlier, for a slight sketch, of the subject.

I shall here therefore only notice such statements as Jacquin has either omitted or imperfectly given, and continue the history to the present time.

In 1763, Adanson correctly describes the stamina in Asclepias as having their filaments united into a tube surrounding the ovaria, their antheræ bilocular and cohering with the base of the stigma, and the pollen of each cell forming a mass composed of confluent grains as in Orchideæ. He is also correct in considering the pentagonal body as the stigma; but he has entirely overlooked its glands and processes, nor does he say anything respecting the manner in which the pollen masses act upon or communicate their fecundating matter to it.

In 1779, Gleichen†, although he expressly says that in young flower buds the pollen masses are distinct from those glands of the pentagonal central body to which they afterwards are attached,

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* *Phytotomie.*

† *Microscop. Entd.* p. 73, et seq.

tached, yet considers both masses and glands as equally belonging to the anthera, the mass being the receptacle of the pollen. He further states that before the masses unite with the glands they are removed from the cells in which they were lodged, and are found firmly implanted by their sharp edge into the wall of the tube which surrounds the ovaria; that in this state a white viscid substance hangs to them, which when highly magnified appears to consist of very slender tubes containing minute globules; and these tubes with their contents he considers as constituting the early preparation for the formation of pollen. He also asserts that the tops of the styles are not originally connected with the pentagonal body to which the glands belong,—the stigma of Adanson, Jacquin, and others; and that therefore the true stigmata are those extremities of the styles on which, he adds, vesicles and threads are observable. And lastly, he supposes that impregnation, which he says is of rare occurrence in this family, does not usually take place until those stigmata have penetrated through the substance of the pentagonal body, and are on a level with its apex; at the same time he is disposed to believe that insects may occasionally assist in this function, by carrying the fecundating matter directly to the stigmata, if I understand him, even before they enter the pentagonal body. His conclusion therefore is, that in Asclepiadeæ impregnation may be effected in two different ways.

This description, in several respects so paradoxical, and of which Jacquin has overlooked some of the most important parts, is too remarkable to be here either omitted or abridged. It is not indeed strictly correct in more than two points, namely, in the pollen masses being originally distinct from the glands, and in the masses, when found implanted in the membrane surrounding the ovarium, having minute tubes filled with granular matter hanging to them. The remaining statements, however, though essentially erroneous, are so far founded in fact, that had Gleichen either opened or rather dilated the opening which must have existed in the pollen mass when these tubes were found hanging to it, and more carefully attended to the state of the other parts of the flower when the mass was seen implanted in the tube, he must necessarily have obtained a correct view of the whole structure, and consequently have greatly advanced,—by at least half a century,—not only our knowledge of this particular family, but also the general subject of vegetable impregnation.

In 1793, Christian Konrad Sprengel, who adopts the opinion of Jacquin both with respect to the pollen masses and pentagonal stigma, further states, that this stigma has a secreting upper surface or apex, and is formed of two united bodies, each of which conveys to its corresponding ovarium the fecundating matter, consisting of the oily fluid which exudes from the surface of the pollen mass. He also considers insects as here essentially necessary in impregnation, which they effect by extracting, in a manner particularly described, the pollen masses from the cells, and applying them to the apex of the stigma. And lastly, as extraordinary activity of the insect is necessary, or at least advantageous in the performance of this operation, that activity is, according to him, produced by the intoxicating secretion of the nectaria*.

In 1809, an essay on Asclepiadeæ was published in the first volume of the Memoirs of the Wernerian Natural History Society, in which one of my principal objects was to establish the opinion, more or less conjectural, of Adanson, Richard, Jussieu, and Schreber, respecting the structure of the stamina and stigma. With this view I appealed to the remarkable fact, that in the early state of the flower-bud the pollen masses are absolutely distinct from the glands and processes of the stigma, to which they in a more advanced stage become attached. This proof of the real origin of parts I then believed to be entirely new. It has however been already seen that the fact was noticed by Gleichen, and it will presently appear that it was also well known to another original observer.

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* It may here be remarked, that the prevailing form of inflorescence in Asclepiadeæ is well adapted to this economy; for the insect so readily passes from one corolla to another, that it not unfrequently visits every flower of the umbel.

In the essay referred to, I had not very minutely examined the texture of the pollen mass, and in true Asclepiadeæ I had failed in ascertaining its real internal structure; not having been then aware of the existence of the included grains of pollen, but believing, until very lately, that the mass in its most advanced state consisted of one undivided cavity, filled with minute granular matter mixed with an oily fluid; and hence concluded that the fecundating matter was conveyed from the mass through the arm and gland to the stigma.

In the month of April last I saw, for the first time, drawings of several Asclepiadeæ made between 1805 and 1813 by Mr. Bauer, who, aware of the interest I took in this subject, with his accustomed liberality and kindness, offered me any part of them for publication.

Among these drawings, exceeding perhaps in beauty and in the completeness of the details all the other productions with which I am acquainted even of this incomparable artist, an extensive series, exhibiting the gradual development of the parts of the flower in *Asclepias curassavica*, were the most important.

In this series, made in 1805, and commencing when the pollen is just separable in a pulpy mass from its cell, the glands of the undivided stigma being still invisible, the fact of the distinct origins of these parts is very satisfactorily shown, in accordance with my observations in the essay referred to*.

But in these drawings Mr. Bauer has gone further than I did, having also represented the internal structure of the pollen mass as cellular; each cell in the flower-bud just before expansion being filled with a grain of pollen, marked with lines indicating its quaternary composition; while in the expanded flower this grain is exhibited as shrivelled, having discharged its contents, which consist of a mixture of an oily fluid and minute granules. From this, the concluding stage of the series, it may be inferred that Mr. Bauer's opinion respecting the mode of impregnation in Asclepiadeæ agrees with that which I had adopted, and which, though probably originating with Richard in 1779†, and briefly stated by him in 1802‡, was first distinctly expressed as a conjecture in 1789 by M. de Jussieu.

In 1817, Mr. Stephen Elliott states that he observed, in his *Podostigma*§,—a genus nearly allied to Asclepias,—a fibre or cord extending through the centre of the corpuscular pedicel or attenuated base of the stigma, and communicating from the anthera to the ovarium. He adds, that Dr. Macbride has since seen it in some species of Asclepias.

There can be no doubt that the cord here noticed is of the same nature with that which Gleichen has described in a different state, and of which I shall presently have occasion to speak.

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* In a flower-bud much earlier than the commencement of Mr. Bauer's series I have found the pistilla to consist merely of two distinct very short semicylindrical bodies, the rudiments no doubt of the future stigma.

In this stage also the antheræ are flat, nearly orbicular or ovate, greenish, rather thick and opake, but petal-like, with no inequality of surface, or any other appearance of the future cells, which in a somewhat more advanced stage are indicated by two less opake areolæ, and at the same time the two semicylindrical bodies unite to form the stigma. (Pl. 36. fig. 7—11.)

† *Encycl. Botan.* i. p. 212.

‡ *Bulliard, Dict. de Bot.* ed. 2. p. 56.

§ *Bot. of Carol. and Georg.* i. p. 327.

In 1824, Professor Link*, while he admits the distinct origins of the pollen masses and glands or corpuscula seated on the angles of the stigma, yet considers both these parts as equally belonging to the anthera. In this respect his opinion is identical with that of Gleichen. The pollen mass, he adds, is composed either of a cellular tissue, or manifestly of grains of pollen: the former part of the description being no doubt meant to apply to true Asclepiadeæ, the latter to Periploceæ.

Professor L. C. Treviranus in 1827† published some observations on this family, in which his account of the structure of the pollen differs in several points from that exhibited in Mr. Bauer's drawings, which he states he had seen three years before this publication.

In *Asclepias curassavica*, the species more particularly examined by Treviranus, he describes the pollen mass as filled with compressed, nearly round but obtusely angular, colourless, simple grains, containing minute granules; the pressure of the external grains, or those in contact with the general covering, giving it the appearance of being cellular.

In speaking of the mode of impregnation, he says, that the pollen mass, at the time when its connexion is established with the process or arm of the gland, which is then very viscid, undergoes manifest changes, from being ventricose and opake becoming flat, hard, and transparent. These changes he thinks are probably owing to the extraction of its fecundating matter by the process through which it passes to the glands, and by them to the angles of the stigma, whence it may be easily communicated to the styles and ovaria. His opinion, therefore, in every respect agrees with that which originated with Richard and Jussieu, and which I had adopted.

The celebrated traveller and naturalist, Dr. Ehrenberg, in

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* *Phil. Bot.* p. 300.

† *Zeitsch. f. Physiol.* ii. p. 230.

1829* has given a very interesting account of the structure of the pollen masses in Asclepiadeæ, from observations commenced in 1825, and others made in 1828.

In this account he describes the pollen mass as consisting of a proper membrane bursting in a regular manner, the cavity being not cellular but undivided and filled with grains of pollen, each grain having a cauda or cylindrical tube often of great length, and all these tubes being directed towards the point or line of dehiscence. This appendage or cauda he considers analogous to the *boyau* of Amici and Brongniart, differing however in its forming an essential part of the grain in Asclepiadeæ; whereas in other families the application of an external stimulus is necessary for its production.

He is entirely silent as to the manner in which these caudate grains communicate with or act upon the stigma; and does not in any case remark,—what must, I think, have been the fact, at least in several of the plants in which this structure was observed, and especially in those with pendulous pollen,—that the mass examined was no longer in the cell of the anthera, but had been removed and probably applied to some part of the stigma.

In the month of July last I examined several species of Asclepias, with reference to Mr. Bauer's drawings and Dr. Ehrenberg's account of the pollen;—the first object, therefore, was to ascertain the structure of the pollen mass.

Although on this subject my earliest observations essentially agreed with Mr. Bauer's figures of the mass, which represent it as having a subdivided cavity with a grain of pollen in each cell; yet a further examination had led me to adopt the opinion of Treviranus and Ehrenberg, who describe its cavity as being undivided and filled with distinct grains.

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* *Linnæa* iv. p. 94.

I was confirmed in this opinion on considering the state of the mass after the production of the pollen tubes: for it appeared very improbable that the cells, unless they were of extreme tenuity, could be either suddenly removed or sufficiently ruptured to admit of the passage of the tubes from its more distant parts to the point or line of dehiscence.

The appearance however occasionally met with, of lacerated membranes proceeding, as it seemed, from the margins of the areolæ of the inner surface of the mass, added to the facts which had originally led me to adopt Mr. Bauer's view, determined me to re-examine the subject.

The result of this examination, made on specimens of *Asclepias phytolaccoides* and *purpurascens*, but especially the former, proved that the mass in these species is really cellular in all stages, as Mr. Bauer has represented it in *A. curassavica*, and that in the advanced flower-bud, as in the expanded flower, the cells may be seen, though not without difficulty, after their grains are removed.

The pollen mass in several species of Asclepias, particularly in *Asclepias phytolaccoides** (and in *A. curassavica*, as figured by Mr. Bauer), consists of cells disposed in three series parallel to its sides, the middle series being often more or less interrupted.

The cells of the outer layer of each side have their opposite walls very unequal both in colour and thickness. The outer wall of each of these cells, which is formed by one of the areolæ of the surface, is of a deep yellow colour, nearly opake, and of such thickness as to prevent external bursting; the inner is of a paler yellow, semi-transparent, and so much thinner as to determine internal rupture, which in these cells, after the production of the tubes, seems to take place without regularity, and to such an extent, that after the removal of the grain the remains of the inner wall are not very readily distinguishable.

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* Tab. 35. fig. 8.

Sections of the mass indeed, both transverse and longitudinal, exhibit an appearance of cellularity; but there is here a source of fallacy, unless the contained grains are also visible in the section: and the best proof of its being cellular is derived from the state of the central or middle series after the bursting of the mass.

The cells of this central layer are of equal thickness throughout, and on the production of the tubes burst in a definite manner towards the convex edge of the mass, and at the same time generally separate from each other. They continue however to inclose the grain, or, as it may be considered, the inner membrane of the grain of pollen, whose outer membrane is formed by the cell itself; and the tenacity of this outer membrane is such that it may easily be removed from the inner without further apparent rupture.

These central grains, thus covered by their respective cells, may readily be distinguished, by their pale yellow colour and a certain degree of opacity, from the naked grains or inner membranes, which, like their tubes, are entirely colourless, and transparent*.

In Asclepiadeæ, therefore, it may be said that the greatest development of the pollen grain exists; namely, a grain having an undivided cavity, whose membranes are entirely distinct, and the pollen tubes of which seem to possess the highest degree of vitality yet met with.

In the perfectly developed state of the pollen mass, the grain, considered as distinct from its outer membrane or containing cell, is nearly round, but slightly and obtusely angular, much compressed, with an undivided cavity, and exhibiting no indication of its being composed of four or any other number of united cells. Its membrane is transparent and colourless, made up of two united coats, and the cavity is filled with spherical granules of nearly uniform size, among which a few oily particles are occasionally observable*. In this state no appearance or indication of the tubes or appendages described by Dr. Ehrenberg is found.

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* Tab. 35. fig. 9.

On the 16th of July, in repeating my examination of *Asclepias purpurascens*†, I observed in several flowers one or more pollen masses removed from their usual place, namely the cell of the anthera, and no longer fixed by the descending arm to the gland of the stigma, but immersed in one of the fissures formed by the projecting alæ of the antheræ, and in most cases separated from the gland, a small portion of the arm or process, generally that only below its flexure, remaining attached to the mass‡.

In the cases now described, the mass, which in general is entirely concealed by the alæ, was so placed in the fissure, that its inner or more convex edge was in contact with the outer wall of the tube formed by the united filaments, and the gibbous part of the edge closely pressed to that point where this tube is joined to the base of the corresponding angle of the stigma§.

These masses, at the point of contact, in most cases adhered firmly to the tube or base of the stigma, and on being separated, a white cord or fasciculus of extremely slender threads or tubes, issuing from the gibbous part of the edge, which had then regularly burst, came into view.

On laying open the pollen mass,—which in this state was easily done, by first dilating the aperture that gave issue to the cord,—each of the tubes composing it was found to proceed from a grain of pollen. These grains retained nearly their original form, but were become more transparent, and had generally lost a great portion of their granules; and these granules were not often to be found even in the tube, especially after it had acquired considerable length*.

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* Tab. 34. fig. 6; and Tab. 56. fig. 3, & 13.

† Tab. 34.

‡ Tab. 35. fig. 2, 3, 4, & 7.

§ Tab. 34. fig. 7.

Almost every grain in the mass had produced its tube, and the tubes were directed from all parts of it towards the point of dehiscence. In this state the mass had become more convex from the increased bulk of its contents.

The tube so produced from each grain of pollen cannot be said to be emitted from it, but is manifestly an elongation of its membrane. These tubes are transparent, cylindrical, about 1-2000th of an inch in diameter, neither branched nor jointed, with no apparent interruption in their cavity, and when of great length, which they often attain, are frequently without granular matter.

I next proceeded to examine the course of the cord, which in most cases,—and indeed in all where the mass had remained a sufficient length of time in the fissure,—had opened a passage for itself through the membrane, or rather had separated the upper edge of this membrane from the base of the stigma, to which it was before united. Having effected this separation, it was found to proceed along the surface of the base of the stigma in a line exactly opposite to the glands seated on the apex of the same bevelled angle. The cord having passed along the surface of the attenuated base of the stigma until it arrives at its articulation with the two styles, then inclines towards the inner side of the apex of the style nearest to it, and actually introduces itself, wholly or in part, into the hollow of the apex, which in this stage is in some degree exposed†. But as the partial separation of the styles from the stigma, then taking place, is not always sufficient for the free admission of the whole cord, a few of the tubes not unfrequently become bent, in some cases even zigzag, doubtless in consequence of the obstacles opposed to them; and such tubes very seldom enter the style, but along with others hang down externally below the joint. This introduction of part of the tubes into the apex of the style is soon followed by a manifest enlargement of the ovarium, and of the style itself, which, in *Asclepias purpurascens*, then exhibits a discoloured blackish line, visible even on the surface of its inner side. On opening the cavity or body of the style in this stage, a fasciculus of tubes was constantly seen passing down the centre, which was originally pulpy, and the walls of the cavity formed by the passage of these tubes was always found indurated and blackened, having every appearance of being absolutely killed.

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* Tab. 35. fig. 7, & 10; and Tab. 34. fig. 12.

† Tab. 34. fig. 7—9; and Tab. 35. fig. 4, & 10.

I have never been able hitherto to follow these tubes further than the commencement of the placenta, where they really appear to terminate*. I have not at least yet succeeded in tracing any of them either on the surface or in the substance of the placenta, though with this object I have examined it not only in its first degree of enlargement, but also in some of its more advanced stages.

The same series of appearances, with very slight modifications only, were observed in all the species of Asclepias (not indeed more than seven in number) which I had opportunities of examining during the summer. For in those species in which the pollen mass was not found transferred from its original position to the fissure, and in contact with the base of the style, no doubt by means of insects, it was not difficult to place it there; and in doing so I never failed to obtain the same results.

I now turned my attention to the base of the stigma, expecting to find there such a modification of surface as might serve to account for the rupture and production of the tubes in the mass brought in contact with it. I have, however, in no case been able to observe the slightest appearance of secretion, or any difference whatever in texture, between that part and the general surface of the stigma.

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* Tab. 34. fig. 10, & 11; and Tab. 35. fig. 5, & 6.

The bursting of the mass in Asclepias is uniformly on the more rounded edge; and this, it may be observed, is the inner edge or margin of the mass, with reference to the cell of the anthera in which it is formed; and I may further remark, that in the only case in which I have hitherto observed dehiscence in an erect pollen mass, namely, in *Hoya carnosa*, it also takes place along the inner margin.

In Asclepias the bursting always commences at the most prominent point of the convex edge, and to this part it is generally confined: it is sometimes however found extending through the greater part of its length.

On carefully examining the convex edge, and more particularly its most prominent portion, I have not been able to observe in it any change or peculiarity of texture, or even any obvious difference in the form of the meshes of the reticulated surface. Notwithstanding this apparent want of secretion in the base of the stigma, and of difference of texture in the covering of the mass of pollen at the point where it comes in contact with that organ, it must still be supposed that there is some peculiarity both in the surface of the stigma and in the prominent edge of the mass, on which the effects in question depend.

These effects are indeed very remarkable; the stimulus here supposed to be derived from the surface of the stigma, and applied to the prominent point of the convex edge of the pollen mass, producing its appropriate action not only in those cells or grains of pollen in immediate contact with that point, but generally in every grain in the mass. But as there are no visible conductors of this stimulus within the mass, it must either be supposed to be propagated from one cell to another, or conveyed from the prominent point of the edge to every other part of the surface of the covering itself.

To ascertain whether contact of the convex edge of the pollen mass with this point of the stigma was absolutely necessary for the rupture of the mass and the production of tubes, I in the first place introduced a mass into the fissure, but with its convex edge outwards. In this position no change whatever took place.

I next removed one of the glands of the angles of the stigma, and applied the convex edge of a mass to the surface thus exposed, which even in this stage—to facilitate the removal of the gland by insects—continues to secrete. In this case, dehiscence and protrusion of pollen tubes did follow, more slowly however, and less completely, than when brought in contact with the non-secreting base.

On applying the pollen mass of one species of Asclepias to the base of the stigma of another, the usual changes generally took place; but still, as it seemed, less perfectly, and only after a longer interval.

Pollen masses of *Asclepias purpurascens* being applied to the stigma of *Epipactis palustris*, and immersed in its viscid secretion, the dehiscence, contrary to expectation, not only took place, but even more speedily than usual, that is within twenty-four hours. Some of the grains were also found discharged from the mass unchanged, while others, both discharged and still inclosed, had begun to produce tubes.

The greater number of these observations were also made with *A. phytolaccoides*, which, on account of the greater size of its flower, I at first preferred. I found, however, with reference to such experiments, an objection to employing this species, arising from the great excitability, so to speak, of its mass, which in some cases produced its tubes merely on continued immersion in water. I even found that in this species, in the gradual decay of the flower, where the parts remain soft, the rupture and protrusion of tubes took place while the mass was still in its original position, immersed in the cell of its anthera*. The tubes produced in this situation often acquire a great length, but coming, immediately on their protrusion from the mass, in contact with the membrane of the anthera, their course is necessarily altered; and in their new direction, which is generally upwards, they not unfrequently arrive at the top of the cell, or even extend beyond it.

In addition to the several species of Asclepias already referred to, *Cynanchum* (*Vincetoxicum*) *nigrum* is the only plant of this family in which I have observed the whole of the appearances; namely, the rupture of the mass, the production and protrusion of the pollen tubes, their union into a cord, with the course and entrance of this cord into the cavity of the style.

The present essay therefore, as far as regards this family, might with greater propriety have been entitled, "On the mode of impregnation in the genus Asclepias." It seems, however, allowable to conclude, that in all the genera having pendulous pollen masses, the same economy, slightly modified perhaps in some cases, is likely to be found. But among those with erect pollen masses, there are several in which more considerable differences may be expected. Of this section of the family I have hitherto had the opportunity of submitting only one plant to careful examination, namely, *Hoya carnosa;* and even here my observations are incomplete.

In *Hoya carnosa* I have never found the pollen tubes produced, or masses ruptured, while remaining in their original position; but I have succeeded in producing these effects by bringing them in contact with certain parts of the corona.

The rupture and protrusion of pollen tubes, then, take place through the whole length of the inner edge of the mass, which, as in all the genuine species of Hoya, is truncated and pellucid*. But I have not yet been able so to place the mass as to produce a cord of tubes communicating with the stigma, nor can I at present conjecture how this is to be effected.

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* Tab. 35. fig. 11.

I shall conclude with some observations equally relating to both the families that have been treated of.

It is in the first place deserving of remark, that while Asclepiadeæ and Orchideæ so widely differ in almost every other respect, there should yet be an obvious analogy between them in those points in which they are distinguished from all other Phænogamous plants.

It is unnecessary here to state the numerous and important differences existing between these two families: but it may be of some interest to make a few remarks on their points of agreement or analogy.

These are chiefly two: The first being the presence of an apparently additional part, not met with in other families; the second, the cohesion of the grains of pollen, and their application in masses to the female organ.

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* In the tubes of *Hoya carnosa* I have been able to confirm Professor Amici's observation with respect to circulation taking place in the *boyaux* of the grains of pollen. In this case the membrane being very transparent, and the granules, before the tube has acquired any considerable length, not being so numerous as to obscure the view of the opposite currents, they were very distinctly seen.

I have also observed circulation in the pollen tubes in a few other cases; especially in *Tradescantia virginica,* in which, while the tube was still very short, the circle partly existing in the tube was completed in the body of the grain. The circular current in grains of pollen before the production of the tube may likewise, in some cases, but not very readily, be distinguished, as in *Lolium perenne.*

It might perhaps be supposed that the molecular motion, which in a former essay I stated I had seen within the body of the grain of pollen, might have been merely an imperfect view of the circulation of granules, and such I am inclined to think it really was in *Lolium perenne*.

I have however also very distinctly seen within the membrane of the grain of pollen in some species of Asclepias, vivid oscillatory motion of granules without any appearance of circulation.

With regard to the first peculiarity it may be observed, that there is no real addition made to the number of organs in either family, and that in both families the apparent addition consists in a modification or production of the stigma; the modified part of which loses the proper function of that organ.

This production of the stigma,—which is generally present, and wanting only in certain Orchideæ, where its place is sometimes supplied by an analogous modification of the male organ,—though differing very remarkably in appearance in the two families, agrees in being originally distinct from the pollen masses, and in the advanced stage becoming firmly attached to them; in adhering but slightly to the point of its formation after the attachment to the pollen takes place; and in being so constructed as to be readily removed by insects from its original position along with the pollen masses.

As to the second point of agreement; namely, the cohesion of the grains of pollen into masses of considerable size, and the application of these masses to the stigma,—it is obviously connected with that which might perhaps be termed a third peculiarity; the apparent necessity for an unusual number of pollen tubes which are to act in concert; in the one family to penetrate to and regularly arrange themselves in the cavity of the ovarium*; in the other, to open a communication with the stigma, and then to pass along a non-secreting surface, until they arrive at a distant point, where they are to be introduced into the cavity or body of the style.

With respect to the agency of Insects in fecundation in those two orders, there can be no doubt that it is very frequently employed in Orchideæ; at the same time there are evidently cases in that family in which, from the relative position of the organs, the interposition of these agents is not always required. But in those Asclepiadeæ at least that have been fully examined, the absolute necessity for their assistance is manifest.

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* See Additional Observations.

Two questions still remain.

The first regards the proof of the actual penetration of the pollen tubes into the cavity of the ovarium in both families.

In Asclepiadeæ I shall only observe, that I consider the evidence complete; but in Orchideæ it may be admitted that it is not altogether so satisfactory. Of the descent of pollen tubes through the cavity of the stigma in Orchideæ, the evidence appears to me unquestionable. With respect, however, to the origin of the cords formed of similar tubes, so numerous and so regularly arranged in the cavity of the ovarium, and which are in contact with surfaces not altogether incapable of secretion, it might perhaps be alleged, either that they wholly originate from the supposed conducting surfaces, or that they consist of a mixture derived from both sources.

That mucous threads, or capillary tubes, in most respects similar to pollen tubes, and certainly altogether belonging to the style, exist in some plants, there is no doubt; and such I have observed in Didymocarpus, Ipomopsis, and in Allamanda, before the application of the pollen to the stigma. I am still, however, of opinion, that those found in the cavity of the ovarium in Orchideæ are really derived from the pollen*; an opinion which receives some confirmation from the manifest descent of the pollen tubes in the style in many other families, as in several Scrophularinæ, Cistineæ, Viola, and Tradescantia.

The second question is, Whether the granules originally filling the grain of pollen, and which may often be found in the tubes, especially in their nascent state, both in these and in many other families, are the essential agents in the process

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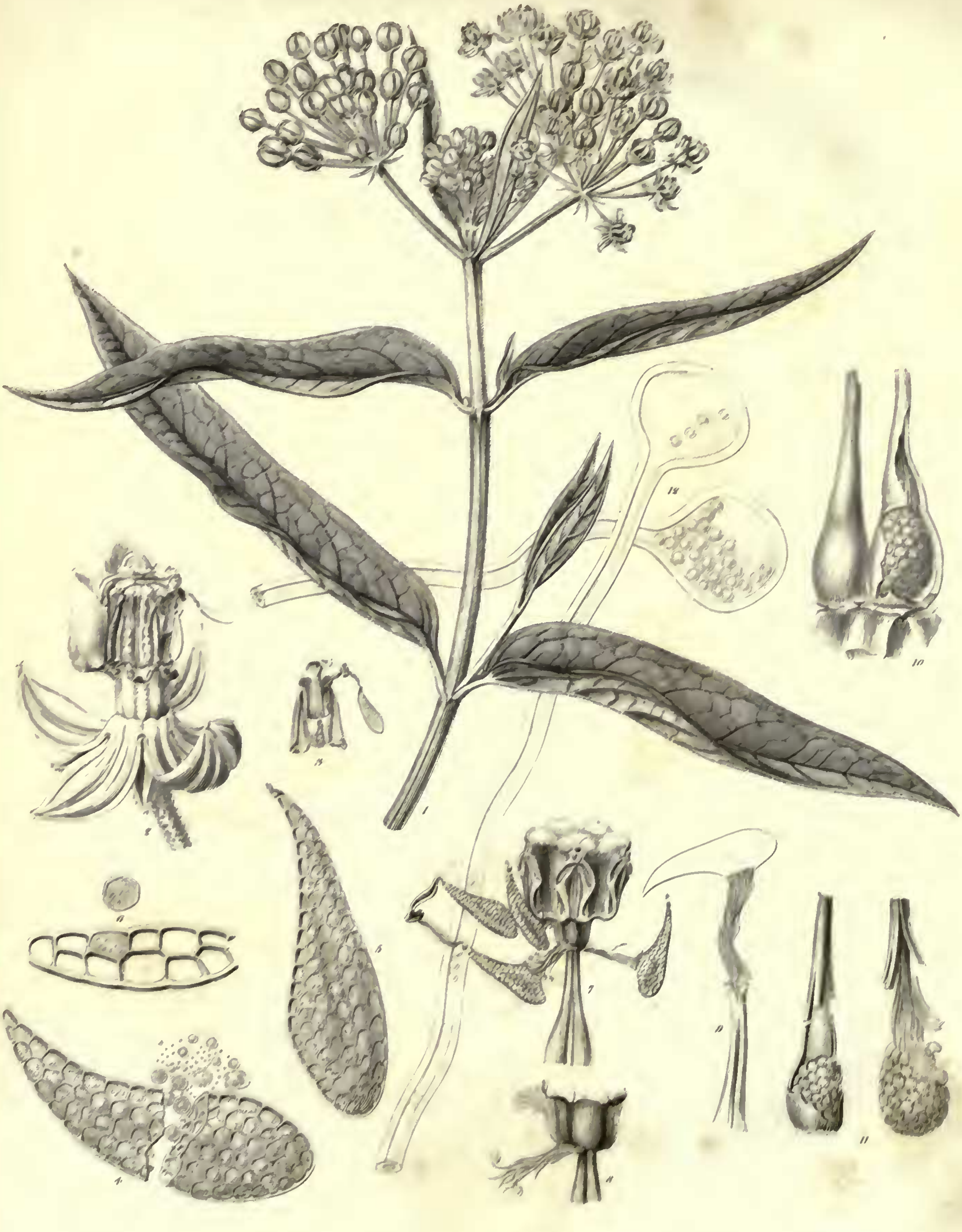
* See Additional Observations.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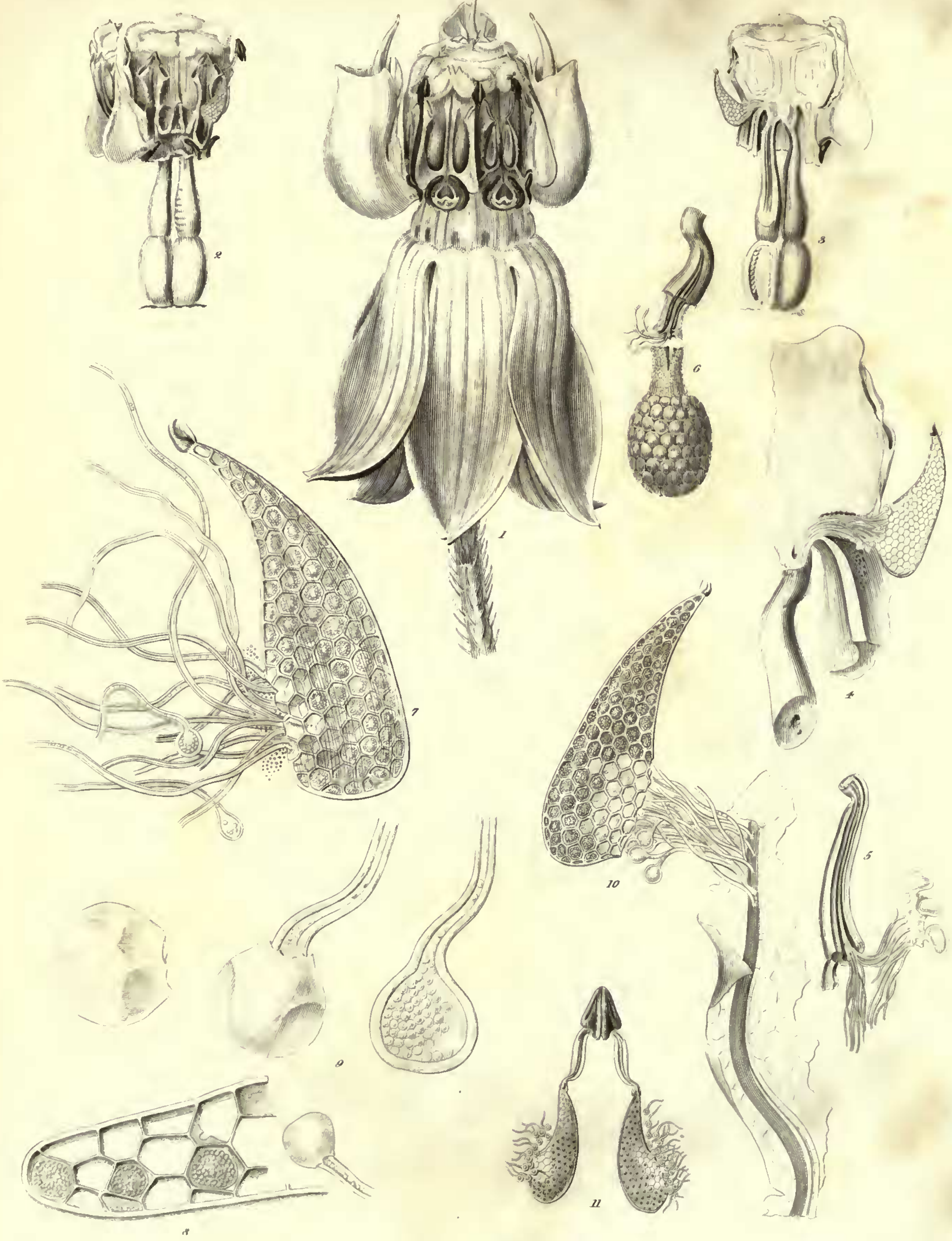
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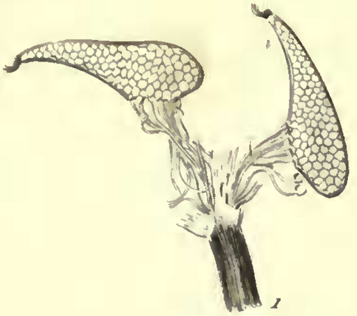
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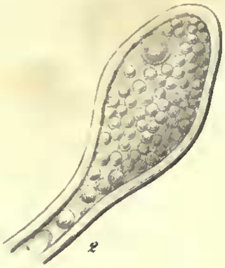
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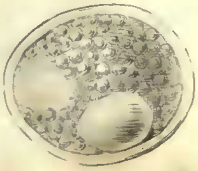
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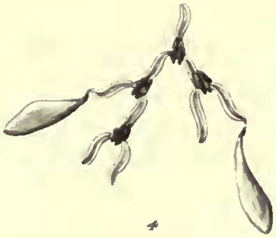
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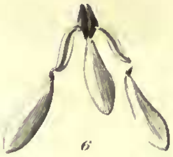
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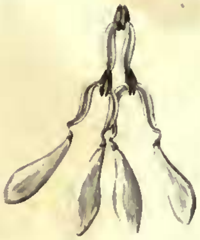
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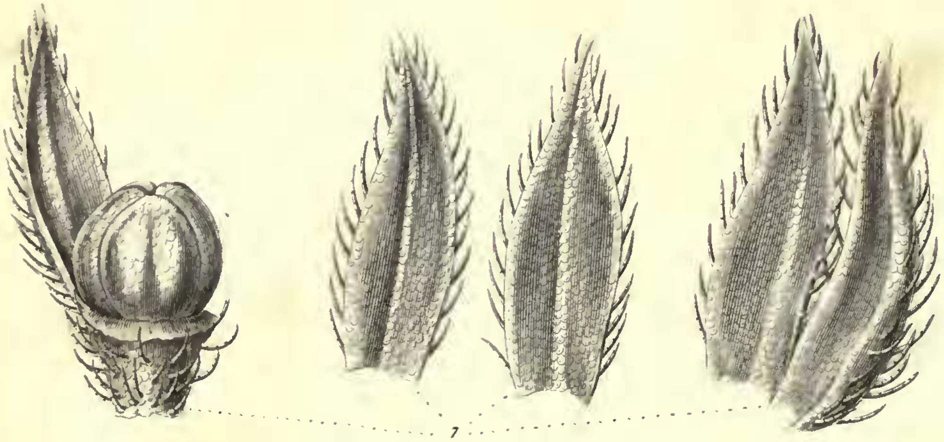
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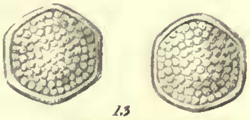
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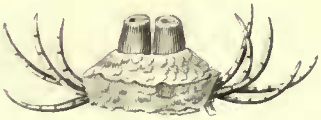
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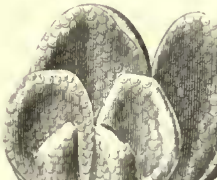
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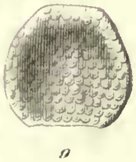
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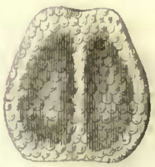
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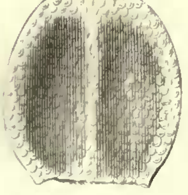
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